OCCURRENCE OF ANISOPHYLLY AND ANISOCLADY WITHIN THE AMARANTHACEAE

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ABSTRACT

Anisophylly and anisoclady, features considered rare in the Amaranthaceae, were observed within some members of the subfamily Gomphrenoideae (Amaranthaceae) during collection of specimens for molecular phylogenetic analysis. Phyllotaxy, equality of leaf size in opposite leaves at a single node, and branching pattern were surveyed within the family to determine their occurrence and potential taxonomic utility. Taxonomic occurrence of anisophylly and anisoclady within Amaranthaceae and the potential significance of their presence are discussed.

RESUMEN

La anisofilia y la anisocladia, características consideradas raras en las Amaranthaceae, fueron observadas en algunos miembros de la subfamilia Gomphrenoideae (Amaranthaceae) durante la recolección de especimenes para análisis filogenéticos moleculares. Se estudió la filotaxis, igualdad de tamaño en hojas opuestas en un nudo, y patrón de ramificación en la familia para determinar su presencia y su potencial utilidad taxonómica. Se discute la presencia de anisofilia y anisocladia en las Amaranthaceae y el significado potencial de su presencia.

INTRODUCTION

Anisophylly refers to the insertion of leaves of different sizes along a stem. The anisophyllous condition is often found on stems exhibiting plagiotropy (horizontal growth) and anisoclady, the differential development of axillary buds along a stem (Dengler 1999). Anisophylly is prevalent among tropical plant families with a decussate leaf arrangement (e.g., Acanthaceae, Gesneriaceae, Melastomataceae, Rubiaceae, and Urticaceae) as well as among some temperate trees such as *Acer* L. and *Populus* L. (Sanchez-Burgos & Dengler 1988; Dengler 1999).

The Amaranthaceae s.s. is a primarily tropical family of flowering plants consisting of approximately 69 genera and 1,000 species classified in the Caryophyllales (Townsend 1993). Morphologically, the Amaranthaceae is sister to the Chenopodiaceae with which it shares numerous morphological characteristics (Kühn 1993; Townsend 1993; Kadereit et al. 2003; Pratt 2003; Müller & Borsch 2005). Molecular-based phylogenetic studies of the Caryophyllales have shown the Chenopodiaceae-Amaranthaceae alliance to be monophyletic (Manhart & Rettig 1994; Downie et al. 1997; Cuénoud et al. 2002; Pratt 2003; Kadereit et al. 2003; Müller & Borsch 2005). Phylogenetic studies with a large sampling of both Amaranthaceae and Chenopodiaceae support a monophyletic Amaranthaceae within a paraphyletic Chenopodiaceae (Cuénoud et al. 2002; Pratt 2003; Kadereit et al. 2003; Müller & Borsch 2005). The Angiosperm Phylogeny Group (APG) (2003) formally recognized a single family under the name Amaranthaceae for this alliance. For the purpose of this paper, however, we will refer to Amaranthaceae in the strict sense.

The Amaranthaceae has traditionally been divided into two subfamilies (Schinz 1934; Townsend 1993), Amaranthoideae and Gomphrenoideae, based on anther locule number (Table 1). The Amaranthoideae has been further divided into tribes and subtribes (Schinz 1934; Townsend 1993) based on ovule number (Table 1). Phyllotaxy is variable within the Amaranthaceae (Table 1) but alternate leaves are diagnostic for Celosieae

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TABLE 1. Morphological characters of the subfamilies, tribes, and subtribes of Amaranthaceae.

	Anther locules	Ovule Number	Phyllotaxy
Amaranthoideae	4	1–many	Alternate/Opposite
Celosieae	4	many	Alternate
Amarantheae	4	1	Alternate/Opposite
Amaranthinae	4	1	Alternate
Aervinae	4	1	Alternate/Opposite
Gomphrenoideae	2	1	Opposite
Pseudoplantageae	2	1	Opposite
Gomphreneae	2	1	Opposite
Froelichiinae	2	1	Opposite
Gomphreninae	2	1	Opposite

and Amaranthinae in the Amaranthoideae whereas opposite, decussately arranged leaves are diagnostic for Gomphrenoideae (Townsend 1993). The character is polymorphic within Aervinae, occasionally being polymorphic within a population of a single species (Townsend 1993).

While collecting Amaranthaceae in Texas for molecular phylogenetic research on the Chenopodiaceae-Amaranthaceae alliance, it was noted that several genera of Gomphrenoideae (e.g., *Guilleminea* Kunth, *Tidestromia* Standl., and *Alternanthera* Forssk.) appeared to have alternate leaves, an unexpected condition within the subfamily. Further examination of the collected specimens revealed that the taxa in question have opposite leaves, but that the taxa superficially appear alternate-leaved due to a combination of anisophylly and anisoclady. A morphological survey of the family was conducted to determine the prevalence, phylogenetic distribution, and potential significance of these characters within the Amaranthaceae.

MATERIALS AND METHODS

Taxon Sampling.—Herbarium specimens from 24 genera and 52 species of the Amaranthaceae, including members of both subfamilies and all tribes except the monotypic Pseudoplantageae (Gomphrenoideae), were surveyed. Both subtribes of Amarantheae were also sampled. Multiple species were sampled from *Charpentiera* Gaudich and the large genera *Alternanthera, Amaranthus* L., *Gomphrena* L., *Iresine* P. Browne, and *Pfaffia* C. Mart. (Table 2).

Character Sampling.—Phyllotaxy, equality of leaf size between a pair of leaves at a single node, and branching pattern were examined directly from herbarium specimens using a dissecting scope and a modified Pohl's solution (Pratt & Clark 2001) where necessary as follows (Table 3).

- Phyllotaxy was examined from all taxa and recorded as alternate or opposite.
- Equality of leaf size at a single node is inapplicable to alternate-leafed taxa, and was examined only for opposite-leafed taxa. Leaf equality was recorded as isophyllous when both leaves of a pair at a node were of equal size, or as anisophyllous when one leaf of the pair was larger and better developed than the second.

  Leaf equality was quantified by measuring the lengths of leaf pairs from three nodes and calculating the size ratio using the average leaf sizes in opposite-leaved taxa using herbarium specimens (ASTC, ISC, and MO) or digitized computer images (GH, K, and NY). Measurements on digitized images were made only when leaf pairs were unambiguous, a situation that was difficult to measure on anisophyllous taxa. The length ratios were calculated (Table 4) and analyzed using t-Tests assuming both equal and unequal variances with JMP 8.0.1 statistical software (SAS 2002).
- Branching pattern was observed from all taxa and recorded as either isocladic or anisocladic. In taxa bearing opposite leaves, anisocladic branching was recorded for those taxa in which only one bud at a node developed into a branch. Isocladic branching was recorded when both buds at a node developed into branches.

Table 2. Specimens examined. ASTC= Stephen F. Austin State University Herbarium, BPM= Borsch, Pratt, and Müller, GH= Gray Herbarium, ISC= Iowa State Ada Hayden Herbarium, K= Kew Botanical Garden, MO= Missouri Botanical Garden Herbarium, NY= New York Botanical Garden. Numbers in parentheses indicate number of genera/species per indicated taxon (Townsend 1993)

Taxon	Location, collector name and number, herbarium
Amaranthaceae (69/780)	
Amaranthoideae (55/409)	
Amarantheae (50/333)	
Amaranthinae (12/92)	
Amaranthus blitoides S. Wats.	Ames, Iowa, *Pratt 200* (ISC)
Amaranthus retroflexus L.	Ames, Iowa, *Pratt 199* (ISC)
Bosea yervamora L.	Canary Islands, *Kunkel 12484* (MO); Canary Islands, *Bramwell 1326* (MO)
Chamissoa altissima (Jacq.) Kunth	Bolivia, *Nee 40597* (ISC)
Charpentiera obovata Gaud.	Oahu, Hawaii, *Perlman & Lau 6125* (MO)
Charpentiera ovata Gaud.	Maui, Hawaii, *Sohmer 6594* (MO)
Aervinae (38/241)	
Achyranthes bidentata Blume	Ames, Iowa, *Pratt 201* (ISC)
Aerva javonica (Burm. F.) Juss.	Pakistan, *Ajab & Ashraf 1254* (MO)
Calicorema capitata (Moq.) Hook.f.	South West Africa, *Giess, Volk, & Bleissner 6206* (MO)
Nototrichium humile Hillebr.	Oahu, Hawaii, *Degener s.n.* (ISC)
Pandiaka heudelotii (Moq.) Benth. & Hook.	Burundi, *Lambinon 78/84* (MO)
Ptilotus obovatus (Gaudich.) F. Muell.	Australia, *Conn 2285* (MO)
Pupalia lappacea (L.) Juss.	Ghana, *Schmidt, Amponsah, & Welsing 1881* (MO)
Celosieae (5/76)	
Celosia argentea L.	Ames, Iowa, *Pratt 222* (ISC)
Deeringia polysperma (Roxb.) Moq.	Taiwan, *Shu-Hui Wu 1153* (MO)
Hermbstaedtia glauca Moq.	South Africa, *Esterhuysen 240* (MO)
Pleuropetalum sprucei (Hook. F.) Standley	Costa Rica, *Jiménez & Soto 981* (MO); Costa Rica, *Haber & Zuchowski 9397* (MO)
Gomphrenoideae (36/371)	
Alternanthera albida (Moq.) Griseb.	Argentina, *s.c. s.n.* (K)
Alternanthera areqipense Suess.	Arequipa, Peru, *Pennell 13131* (NY)
Alternanthera bettzickiana (Regel) Standl.	Nacogdoches, Texas, *Banks 2046* (ASTC)
Alternanthera brasiliana (L.) Kuntze	Brazil, *Tsugaru & Sano B-223* (NY)
Alternanthera caracasana Kunth	Alpine, Texas, *BPM 3433* (ISC)
Alternanthera ficoidea (L.) R. Br.	Puerto Rico, *Luquillo, Liogier & Liogier 31898* (NY)
Alternanthera morongii Rusby	Asuncion, Paraguay, *Morong 40* (NY)
Alternanthera philoxeroides (Mart.) Griseb.	Chamber Co, Texas, *Jones 1623* (ASTC)
Alternanthera polygonoides (L.) R. Br.	Montgomery Co, Texas, *Raines 258* (ASTC)
Alternanthera pungens Kunth	Carlsbad, New Mexico, *BPM 3449* (ISC)
Alternanthera repens (L.) Kuntze	Hamilton, Texas, *Stanford 1337* (ASTC)
Alternanthera sessilis (L.) R. Br. ex DC.	Concordia Parish, Louisiana, *Thomas, Martin, Scarborough, & Slaughter 106,565* (ASTC)
Alternanthera tenella Colla	St. John, Virgin Islands, *Acevedo-Rodriguez et al. 2913* (NY)
Blutaparon vermicularis (L.) Mears	South Padre Island, Texas, *BPM 3444* (ISC)
Froelichia floridana (Nutt.) Moq.	Mcintosh Co., Georgia, *Duncan 20458* (ISC)
Gomphrena albiflora Moq.	Colombia, *Dawe 527* (K)
Gomphrena arborescens L.f.	Mato Grosso do Sul, Brazil, *Lindman A2497* (NY)
Gomphrena globosa L.	Ames, Iowa, *Pratt 228* (ISC)
Gomphrena lutea Rusby	Ixiamus, Bolivia, *Cardenas 1911* (NY)
Gomphrena pungens Seub.	Minas Gerais, Brazil, *Pirani et al. CRCR8686* (NY)
Gomphrena serrata L.	St. Thomas University, Virgin Islands, *Acevedo-Rodriguez 11372* (NY)
Gomphrena silenoides Chodat	Paraguay, *Hassler 7491* (NY)

TABLE 2. *continued*

Taxon	Location, collector name and number, herbarium
Guilleminea densa (Humb. & Bonpl.) Moq.	Alpine, Texas, *BPM 3434* (ISC)
Gossypianthus lanuginosa (Poir.) Moq.	Tarrant Co., Texas, *Ruth 977* (ISC)
Iresine alternifolia S. Watson	Sonora, Mexico, *Palmer 276* (GH)
Iresine angustifolia Euphrasen	St. John, Virgin Islands, *Acevedo-Rodriguez 2568* (NY)
Iresine argentata (Mart.) D. Dietr.	Coamo, Puerto Rico, *Britton & Britton 9032* (NY)
Iresine diffusa Humb. & Bonpl. ex Willd. var *spiculigera* Eliasson	St. Maarten, Netherlands *Antilles, Mori 26444* (NY)
Iresine grandis Standl.	San Luis Potosi, Mexico, *Pringle 3962* (NY)
Iresine leptoclada (Hook. f.) Henrickson & Sundberg	El Paso, Texas, *Wright 589* (GH)
Iresine orientalis G.L. Nesom	Nuevo Leon, Mexico, *Palmer 1133* (NY)
Pfaffia acutifolia (Moq.) Stutzer	Brazil, *Gardner 2294* (K)
Pfaffia eriocephala Suess.	Neguange, Colombia, *Smith 2095* (NY)
Pfaffia townsendii Pedersen	Goias, Brazil, *Irwin 12611* (NY)
Tidestromia lanuginosa (Nutt.) Standley	Mustang Island, Texas, *BPM 3459* (ISC)

RESULTS

Phyllotaxy.—Phyllotaxy is variable within the family, which possesses both alternate- and opposite-leaved taxa. Within Amaranthoideae, all members of tribe Celosieae and subtribe Amaranthinae were observed to have alternate leaves, however subtribe Aervineae is polymorphic for phyllotaxy, having both alternate- and opposite-leafed taxa. All members of the Gomphrenoideae were observed to have opposite leaves (Table 3).

Leaf Equality.—Anisophylly was observed to occur in some opposite-leaved taxa of Gomphrenoideae (Table 3). One genus, *Alternanthera*, was observed to be polymorphic for isophylly/anisophylly (Table 3). The average leaf length ratio of leaf pairs at a node in isophyllous taxa was 0.94: 1, while the average leaf length ratio of leaf pairs at a node in anisophyllous taxa was 0.59: 1 (Table 4). Inequality of leaves is thus extremely pronounced, with one leaf of a pair measuring nearly twice the size of the second. Two-sample t-Tests were statistically significant at $p < 0.0001$, assuming both equal (DF=31) and unequal (DF= 8.48) variances.

Branching Pattern.—Primary and higher order branching was isocladic in all alternate-leaved taxa. Branching pattern in opposite-leaved taxa was variable, with both isocladic and anisocladic branching patterns occurring within the Gomphrenoideae. Anisocladic branching in opposite-leaved taxa was observed only in taxa with anisophyllous leaves (Table 3). One genus, *Alternanthera*, was polymorphic for branching pattern (Table 3).

Buds developing into branches in anisocladic taxa were always subtended by the larger leaf of the anisophyllous leaf pair. These lateral branches in turn bore opposite, anisophyllous leaves and inflorescences, and could also bear secondary and higher order branches (Fig. 1). Secondary and higher order branches also follow the pattern of anisoclady, as these branches are also subtended by the larger leaf of an anisophyllous leaf pair. Taxa exhibiting anisophylly and anisoclady superficially resemble an alternate phyllotaxy as the larger leaves and their associated branches alternate sides along the axis of the stem (Fig. 1).

DISCUSSION

Anisophylly and anisoclady are fairly common character states within subfamily Gomphrenoideae. Character-state optimizations of phyllotaxy on an independently derived phylogeny based on plastid *ndhF* gene sequence data (Pratt 2003) show that the character has undergone several transitions. Unfortunately, the presence of these states has rarely been noted in the literature, except for the genera *Guilleminea* and *Gossypianthus* Hook. (Henrickson 1987, see especially figures1 A–B and 2 A–C; see also the illustrations in Roberston and Clemants 2003 for *Alternanthera caracasana*, *Guilleminea*, and *Gossypianthus*), nor have the characters been

Table 3. Phyllotaxy, Leaf equality, and Branching in Amaranthaceae. n/a= non-applicable.

	Phyllotaxy	Leaf Equality	Branching
Amaranthoideae-Amarantheae-Amaranthineae			
Amaranthus blitoides	Alternate	n/a	Isocladic
Amaranthus retroflexus	Alternate	n/a	Isocladic
Bosea yervamora	Alternate	n/a	Isocladic
Chamissoa altissima	Alternate	n/a	Isocladic
Charpentiera obovata	Alternate	n/a	Isocladic
Charpentiera ovata	Alternate	n/a	Isocladic
Amaranthoideae-Amarantheae-Aervineae			
Achyranthes bidentata	Opposite	Isophyllous	Isocladic
Aerva javonica	Alternate	n/a	Isocladic
Calicorema capitulata	Alternate	n/a	Isocladic
Nototrichium humile	Opposite	Isophyllous	Isocladic
Pandiaka heudelotii	Opposite	Isophyllous	Isocladic
Ptilotus obovatus	Alternate	n/a	Isocladic
Pupalia lappacea	Opposite	Isophyllous	Isocladic
Amaranthoideae-Celosieae			
Celosia argentea	Alternate	n/a	Isocladic
Deeringia polysperma	Alternate	n/a	Isocladic
Hermbstaedtia glauca	Alternate	n/a	Isocladic
Pleuropetalum sprucei	Alternate	n/a	Isocladic
Gomphrenoideae			
Alternanthera albida	Opposite	Isophyllous	Isocladic
Alternanthera areqipense	Opposite	Isophyllous	Isocladic
Alternanthera bettzickiana	Opposite	Isophyllous	Isocladic
Alternanthera brasiliana	Opposite	Isophyllous	Isocladic
Alternanthera caracasana	Opposite	Anisophyllous	Anisocladic
Alternanthera ficoidea	Opposite	Isophyllous	Isocladic
Alternanthera morongii	Opposite	Anisophyllous	Anisocladic
Alternanthera philoxeroides	Opposite	Isophyllous	Isocladic
Alternanthera polygonoides	Opposite	Isophyllous	Isocladic
Alternanthera pungens	Opposite	Anisophyllous	Anisocladic
Alternanthera repens	Opposite	Anisophyllous	Anisocladic
Alternanthera sessilis	Opposite	Isophyllous	Isocladic
Alternanthera tenella	Opposite	Anisophyllous	Anisocladic
Blutaparon vermicularis	Opposite	Isophyllous	Isocladic
Froelichia floridana	Opposite	Isophyllous	Isocladic
Gomphrena albiflora	Opposite	Isophyllous	Isocladic
Gomphrena arborescens	Opposite	Isophyllous	Isocladic
Gomphrena globosa	Opposite	Isophyllous	Isocladic
Gomphrena lutea	Opposite	Isophyllous	Isocladic
Gomphrena pungens	Opposite	Isophyllous	Isocladic
Gomphrena serrata	Opposite	Isophyllous	Isocladic
Gomphrena silenoides	Opposite	Isophyllous	Isocladic
Gossypianthus lanuginosa	Opposite	Anisophyllous	Anisocladic
Guilleminea densa	Opposite	Anisophyllous	Anisocladic
Iresine alternifolia	Alternate	na	Isocladic
Iresine angustifolia	Opposite	Isophyllous	Isocladic
Iresine argentata	Opposite	Isophyllous	Isocladic
Iresine diffusa	Opposite	Isophyllous	Isocladic
Iresine grandis	Opposite	Isophyllous	Isocladic
Iresine leptoclada	Alternate	na	Isocladic
Iresine orientalis	Opposite	Isophyllous	Isocladic
Pfaffia acutifolia	Opposite	Isophyllous	Isocladic
Pfaffia eriocephala	Opposite	Isophyllous	Isocladic
Pfaffia townsendii	Opposite	Isophyllous	Isocladic
Tidestromia lanuginosa	Opposite	Anisophyllous	Anisocladic

TABLE 4. Leaf length ratios of equal and unequal leaf pairs in Gomphrenoideae.

	Leaf Equality	Leaf Pair Ratio
Alternanthera albida	Isophyllous	0.95 : 1
Alternanthera areqipense	Isophyllous	0.99 : 1
Alternanthera bettzickiana	Isophyllous	0.98 : 1
Alternanthera brasiliana	Isophyllous	0.93 : 1
*Alternanthera ficoidea**	Isophyllous	0.93 : 1
Alternanthera philoxeroides	Isophyllous	1.00 : 1
Alternanthera polygonoides	Isophyllous	0.90 : 1
Alternanthera sessilis	Isophyllous	0.98 : 1
Blutaparon vermicularis	Isophyllous	0.92 : 1
Froelichia floridana	Isophyllous	0.93 : 1
Gomphrena albiflora	Isophyllous	0.97 : 1
Gomphrena arborescens	Isophyllous	0.92 : 1
Gomphrena globosa	Isophyllous	0.96 : 1
Gomphrena lutea	Isophyllous	0.89 : 1
Gomphrena pungens	Isophyllous	0.96 : 1
Gomphrena serrata	Isophyllous	0.94 : 1
Gomphrena silenoides	Isophyllous	0.95 : 1
Iresine angustifolia	Isophyllous	0.93 : 1
Iresine argentata	Isophyllous	0.89 : 1
Iresine diffusa	Isophyllous	0.97 : 1
Iresine grandis	Isophyllous	0.96 : 1
Iresine orientalis	Isophyllous	0.96 : 1
Pfaffia acutifolia	Isophyllous	0.86 : 1
Pfaffia eriocephala	Isophyllous	0.90 : 1
Pfaffia townsendii	Isophyllous	0.97 : 1
Average Leaf Ratio	**0.94 : 1**	
Alternanthera caracasana	Anisophyllous	0.59 : 1
Alternanthera morongii	Anisophyllous	0.54 : 1
Alternanthera pungens	Anisophyllous	0.54 : 1
Alternanthera repens	Anisophyllous	0.57 : 1
Alternanthera tenella	Aniosphyllous	0.68 : 1
Gossypianthus lanuginosa	Anisophyllous	0.54 : 1
Guilleminea densa	Anisophyllous	0.69 : 1
Tidestromia lanuginosa	Anisophyllous	0.56 : 1
Average Leaf Ratio	**0.59 : 1**	

*Average was calculated from only two leaf pairs

used in taxonomic treatments, despite the fact that they may be of some taxonomic utility. The unreported, yet widespread presence of anisophylly and anisoclady within the Amaranthaceae was somewhat surprising, but underscores the great need for critical morphological examination of the Amaranthaceae as well as for its sister family the Chenopodiaceae.

Molecular phylogenetic analyses of the Chenopodiaceae-Amaranthaceae alliance (Pratt 2003; Kadereit 2003; Müller & Borsch 2005) have recovered a strongly supported monophyletic Gomphrenoideae. The relationships of the Gomphrenoideae (opposite leaves) with opposite-leaved taxa of the Aervineae are uncertain. Strict consensus places many of the Aervineae as sister to Gomphrenoideae, although relationships with the Aervineae-Gomphrenoideae clade are currently unresolved (Pratt 2003; Kadereit 2003; Müller & Borsch 2005; Sage et al. 2007). Anisophylly and anisoclady were restricted to the Gomphrenoideae in this survey of the Amaranthaceae. Because the characters have been previously unreported, their presence within a taxon cannot be ruled out based on prior literature.

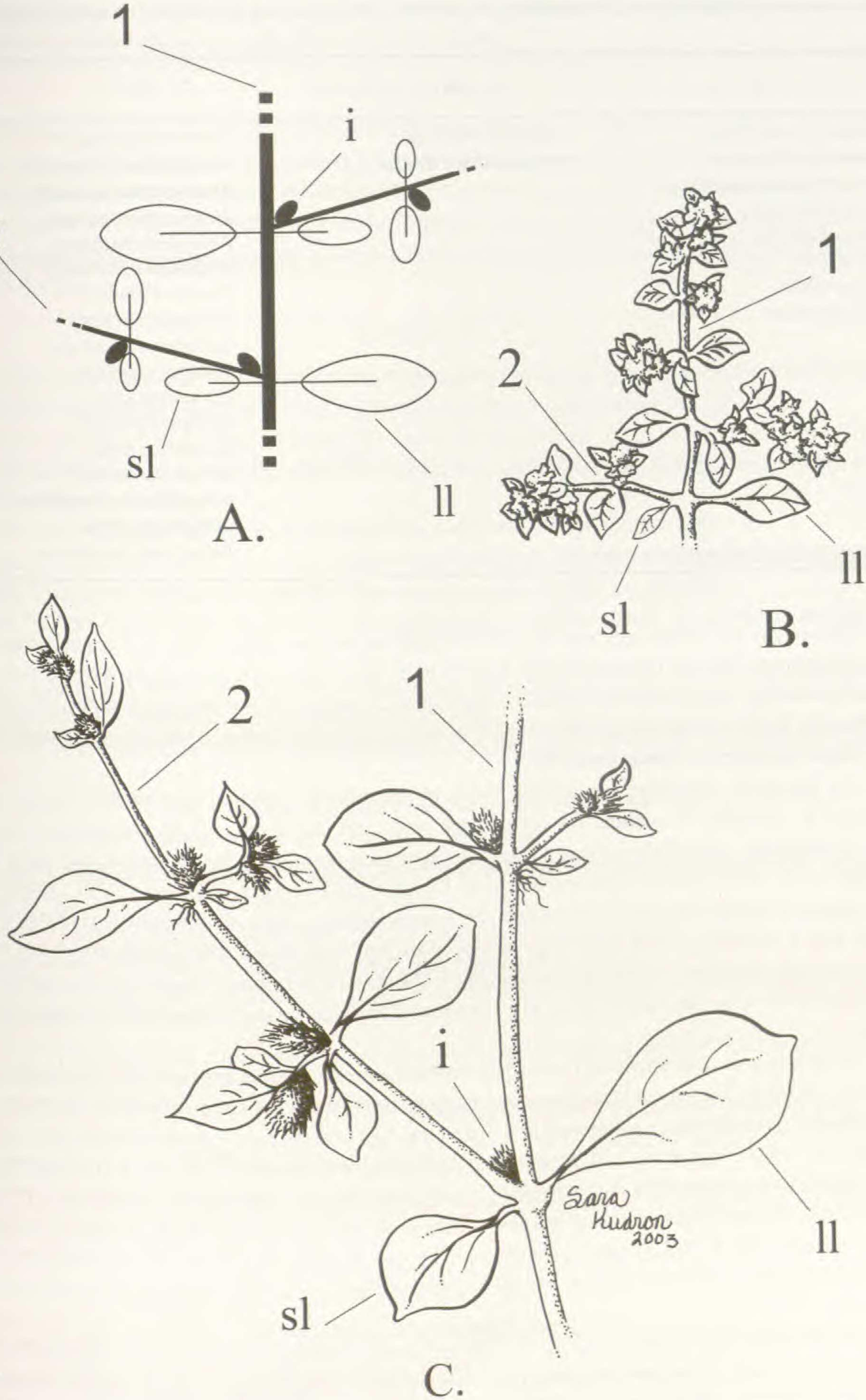

FIG. 1. Diagrams of anisophylly and anisoclady in Amaranthaceae. **A.** Schematic diagram of anisophylly and anisoclady. **B.** *Guilleminea densa*. **C.** *Alternanthera pungens*. ll= larger leaf; sl= smaller leaf; i= flower or inflorescence; 1= primary stem axis; 2= secondary axis.

TABLE 5. Leaf position and photosynthetic patterns in Gomphrenoideae. INT= Intermediate photosynthetic pathway, taxa in boldface= taxa exhibiting anisophylly and anisoclady.

C3	INT	C4
Alternanthera bettzickiana	*Alternanthera ficoidea*	*Alternanthera albida*
Alternanthera brasiliana	***Alternanthera tenella***	***Alternanthera caracasana***
Alternanthera philoxeroides		***Alternanthera morongii***
Alternanthera sessilis		***Alternanthera pungens***
Iresine angustifolia		***Alternanthera repens***
Iresine diffusa		*Blutaparon vermicularis*
Pfaffia acutifolia		*Froelichia floridana*
Pfaffia townsendii		*Gomphrena albiflora*
		Gomphrena arborescens
		Gomphrena globosa
		Gomphrena lutea
		Gomphrena pungens
		Gomphrena serrata
		Gomphrena silenoides
		Gossypianthus lanuginosa
		Guilleminea densa
		Tidestromia lanuginosa

Anisophylly and anisoclady may be taxonomically significant both within and among genera of the Gomphrenoideae. Several other characters known to be associated with anisophylly have yet to be investigated including: stem symmetry (radial vs. dorsiventral); pattern of leaf symmetry (*Selaginella* P. Beauv., *Strobilanthus* Rchb., or *Pellionia* Gaudich. types); anatomy; and developmental pattern (see Dengler 1999 for an in depth treatment of these characters).

The literature designates two general types of anisophylly: habitual anisophylly characterized by anisophylly expressed throughout the entire plant body; and lateral anisophylly characterized by an upright, isophyllous, orthocladic primary axis, the expression of anisophylly and anisoclady being limited to plagiotropic lateral shoots (Sanchez-Burgos & Dengler 1988; Morgan & Dengler 1988; Dengler 1999). Both types of anisophylly may occur within the Amaranthaceae. Habitual anisophylly is characteristic of plants with a creeping growth habit (e.g., *Alternanthera p.p.*, *Guilleminea*, and *Gossypianthus*), and tends to be consistently expressed within species (Dengler 1999). Lateral anisophylly may occur among plants with an upright habit (e.g., *Alternanthera p.p.* and *Tidestromia*) and may be environmentally influenced (Dengler 1999).

The presence of anisophylly and anisoclady within Gomphrenoideae appears to be correlated to photosynthetic pathway. The genera here reported to possess the anisophyllous and anisocladic characters (*Alternanthera p.p.*, *Gossypianthus*, *Guilleminea*, and *Tidestromia*) all possess the C_4 photosynthetic pathway (Table 5; Sage et al. 2007). Sage et al. (2007) report that *Alternanthera* is monophyletic and can be subdivided into a monophyletic C_3 clade and a monophyletic C_4 clade and contains a few species exhibiting an intermediate pathway. Photosynthetic pathway is known (Sage et al. 2007) for eleven of the species of *Alternanthera* examined here. All of the C_3 taxa exhibited isophylly and isoclady, one of the two intermediates had the anisophyllous and anisocladic states, and all but one of the C_4 taxa were anisophyllous and anisocladic (Table 5).

The presence of anisophylly and anisoclady within the Gomphrenoideae bears on hypotheses of their adaptive significance. It has been proposed that these characters are adaptations for increasing light gathering potential in forest understory plants, and in the prevention of self-shading (Dengler 1999). However, all of the plants for which anisophylly and anisoclady are herein reported exhibit the C_4 photosynthetic pathway (Sage et al. 2007), and many are native to xeric environments with bright, full sun. Any hypothesis of the adaptive significance of anisophylly and anisoclady within the Gomphrenoideae must also take into account the correlation of these characters with photosynthetic system.

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